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Relationship Between Forest Decline and Root Health in Ontario Sugar Maple Stands.

By: Cindy Adams, Marika Egyed and Tom Hutchinson. Department of Botany and Institute for Environmental Studies, University of Toronto, Toronto, Ontario, Canada. M5S 1A1.

Abstract

In the past decade sugar maple (*Acer saccharum*) has shown a dramatic and decline in Eastern North America, particularly in southern Quebec where 80% of the trees are affected. Similar, more local declines are also occurring in Ontario, New Brunswick, Vermont, Pennsylvania and New York. We have initiated a study to examine fine root systems of sugar maple in Ontario to determine whether fine root damage is a factor in their present decline. Specifically, we are assessing the health, biomass, mycorrhizal status, branching patterns and chemical composition of roots of healthy and declining mature sugar maples. Preliminary results show an alteration in the intensity of VA infection of declining sugar maple trees, with significantly higher levels of infection in moderately declining trees compared with the levels in healthy trees. Roots of severely declining trees, however, had very low levels of infection. These results, combined with lower levels of calcium in declining sugar maple roots could be important in their present decline. Soils collected under declining trees were lower in Ca, P, Mg and Mn, and elevated in Al, compared with soils from healthy trees. These "declining" soils resulted in a substantial reduction in root growth into ingrowth cores compared with ingrowth cores containing healthy soil.

INTRODUCTION

In eastern North America, Central Europe and Scandinavia the health of forests has declined dramatically over the past decade. The decline is particularly severe for coniferous species at high elevations where acid fogs and elevated oxidants and SO₂ occur frequently, and for European beech, maple, birch and oak at lower elevations. Hardwood tree species at low altitudes have received little attention but recent surveys in Quebec and Ontario have confirmed general suspicions that almost all hardwoods, including sugar maple, red maple, black cherry, white birch, yellow birch, red oak, basswood, beech, and green ash, are showing varying degrees of

dieback. One of the worst affected hardwood species is sugar maple (*Acer saccharum* Marsh.) which has shown a very severe and rapid decline in southern Quebec, affecting up to 80% of the trees at present (Gagnon, personal communication), and more local declines in Ontario (McLaughlin *et al.* 1985), New Brunswick, Vermont, Pennsylvania and New York. Tree death may result in 3-5 years after the onset of symptoms.

In Germany, where the first alarms regarding forest decline were sounded, numerous investigations have attempted to determine the cause of specific forest diebacks and the way in which atmospheric pollutants (acid rain, acid fogs, ozone and SO₂) may be involved. In every instance where root systems were studied, damage to fine roots was observed, including mortality of fine rootlets (Ulrich *et al.* 1980; Murach 1984; Liss *et al.* 1984; Matzner *et al.* 1986), a lower ramification index (i.e. outgrowth of long scarcely branched roots) (Meyer 1987), damage of the endodermis (Hüttermann 1982), abnormal branching (Matzner *et al.* 1986), changes in chemical composition (Bauch and Schröder 1982, Murach 1984), changes in the vertical profile of roots (Murach 1984) and reductions in mycorrhizal infection (Blascke 1986, Vincent 1986).

This paper presents preliminary results of studies conducted to examine fine root systems of sugar maple trees in Ontario in an attempt to determine whether fine root damage is a factor in their decline.

There is already some evidence that the soils in declining sugar maple stands in Ontario and Quebec are inhibiting tree growth. The Ministry of the Environment (MOE) has reported high Al levels associated with fine root mortality in declining trees (McLaughlin 1987). In our laboratory, comparisons between sugar maple seedlings grown on soil collected from beneath healthy or declining mature sugar maples both in Ontario and Quebec, have shown that seedling growth, as well as tissue Ca, Mg, Mn and P is

substantially lower on the "declining" soil, while tissue Al may be elevated (Kinch and Hutchinson unpub.; Hutchinson and Adams unpub.). Consistent reductions in the growth of roots of mature sugar maple trees in "declining" soils were shown in a field experiment using mesh bags (ingrowth cores) filled with soil collected from declining or healthy trees (Adams and Hutchinson unpub.).

These results together with the low pH values in these forest soils (3.5 - 4.5) and probable alterations in soil moisture levels due to loss of foliage, suggest a possible alteration in mycorrhizal status of sugar maple in relation to decline, which in fact constitutes a major hypothesis for forest decline in Europe and North America. Mycorrhiza refers to a symbiotic relationship existing between the roots of vascular plants and a wide range of fungal species, in which the fungal symbiont ameliorates nutrient and water uptake by the plant root system, while assimilates from photosynthesis are transferred from the plant to the fungus (Tyminska *et al.* 1986; Brownlee *et al.* 1983). In addition to the reduction reported in the number of active mycorrhizal tips in declining compared with healthy Norway spruce in Bavaria (Blaschke 1986) and in beech exhibiting symptoms of decline in Germany (Vincent 1986), changes in the mycorrhizal fungal community (Kumpfer and Heyser 1986) and declines of mycorrhizal species of macrofungi (Jansen and van Dobben 1987; Termorshuizen and Schaffers 1987) have been associated with increased acidification of forest stands. Field and laboratory studies, manipulating substrate pH values have reaffirmed the sensitivity of tree mycorrhizal infection to reductions in soil pH (Reich *et al.* 1986; Dighton and Skeffington 1987; Metzler and Oberwinkler 1987; Blascke 1987).

It is known that sugar maple roots should be mycorrhizal at all depths (Kessler 1966). The relationship between the present decline of sugar maple

and fine root damage, especially possible alterations in the mycorrhizal associations has not been studied. Accordingly, the specific objectives of this current study are as follows:

1. To make a detailed assessment of levels of mycorrhizal infection of individual sugar maple in Ontario in relation to the decline status of these specific trees.
2. If a relationship exists between the degree of mycorrhizal infection and tree decline, to establish cause-effect relationships by correlating the degree of mycorrhizal infection with soil pH and soil and foliar chemical levels.
3. To determine whether forest soils collected from under declining and healthy sugar maples differentially influence root health, chemical composition, fine structure and levels of mycorrhizal infection of mature sugar maples. Our previous research, using mesh bags (ingrowth cores) filled with healthy and declining soils, buried around maple trees with a range of decline status' at two Ontario sugar maple sites, showed a substantial reduction in root growth into the bags which contained the declining tree soil.

METHODOLOGY

Only a brief summary of our experimental design and methodology will be presented here. Data are preliminary and incomplete as many aspects of the current study were commenced in May of this year. However, we felt that many of the patterns that were emerging in the data were very interesting and provide some insight into the complexity of the forest decline phenomena. In view of the fact that sugar maple stands are dying at an alarming rate we

hope that this new evidence of altered mycorrhizal symbiosis and root chemistry may spur new research to be initiated before valuable time is lost. Furthermore, the evidence of decreases in soil nutrients in conjunction with increased soil Al levels, adds to the growing evidence that links air pollution to forest decline and to soil acidification. The project consists of two main studies with the following experimental designs:

1. The relationship of mycorrhizal infection of forest trees with soil and foliar chemistry, and soil pH

In the summer of 1987, four Precambrian Shield study sites were established in the Muskoka and Parry Sound Districts of Ontario. The soils of these sites are podzolic, i.e. they are typically acidic and low in nutrient status. Three of these sites are declining sugar bushes (Miller, Ungard and Alf) and the fourth is a healthy control stand (Griffiths). Twenty trees exhibiting a wide range of decline were sampled in each of the declining sites, and twenty trees were randomly selected in the control site. All trees were accorded an index of decline using a detailed rating method that incorporates percentage of dead branches, chlorosis, premature fall colouration and percentage of undersized leaves (after MOE).

Four fine root samples from each of three main roots (i.e. 12 samples) for each tree (i.e. 20 trees/site) were excavated, washed and fixed in FAA for assessment of mycorrhizal infection. To date, only the declining sites, and for these only two-thirds of the root samples, have been assessed for mycorrhizal infection levels.

For all 80 trees described above, soil samples (5 per horizon) were collected from the A₀, A₁ and B horizons and foliage samples from low, medium and high portions of the tree crown were collected in the 1987 field season. Soil samples have all been analyzed for pH but the chemical analyses have not yet been done on either the soils or the foliage.

2. Root ingrowth core study to determine the importance of soil related factors in sugar maple decline

In May, 1986 bulk soil collections were made separately from ten healthy and ten declining trees at two of the declining sugar maple sites used in the first study (Miller and Ungard). These soils were dried and sieved (<2 mm) to remove living and dead roots. Soils were then used to refill corings made around healthy and declining trees at these same sites (a total of 15 trees for the Miller site and 10 trees for the Ungard site). Corings were made to a depth of 10 cm at a distance of 1 m from the tree base, fiberglass screening bags were fitted tightly up against the sides of the hole left by the removed core, and then filled with the test soils. Both healthy and declining soils, as well as steam-sterilized and fertilized treatments of these two soil types were replicated 3 times around each of the sample trees at the two maple sites. The soils for the fertilizer treatment were amended with superphosphate (P_2O_5) and gypsum ($CaSO_4$). The refilled corings were dug out after 8 weeks and the roots which had grown into the bags were recovered by careful washing.

Immediately after the bags were brought back to the laboratory, 2 root samples were taken from each of the 480 root bags and fixed in FAA for future assessment of mycorrhizal infection. Some roots were also fixed in glutaraldehyde and osmium for sectioning and examination of the fine structure using transmission electron microscopy.

Soil and tissue (root and foliage) chemistry

Soil samples were analyzed for pH using the distilled water/slurry and $CaCl_2$ methods. Following nitric acid digestion of roots and foliage, and nitric and perchloric acid digestion of soils, chemical analysis (P, Ca, Mg, K, B, Mn, S and Al) of samples was done using either ICP (inductively-coupled plasma emission spectroscopy) or atomic absorption spectroscopy. N was

determined using a LECO CHN analyzer. Distilled water-extractable (i.e. an estimate of plant available) levels of these same elements were also determined for soil samples.

Microscopy

Fine root samples were fixed in FAA, cleared and stained for vesicular arbuscular mycorrhiza (VAM, the type of mycorrhiza formed in sugar maple roots) using a modified Trypan Blue staining procedure (Phillips and Hayman 1970). Root samples, mounted on glass slides and gently squashed under glass coverslips, were scored for percent mycorrhizal infection, as well as for the presence of non-mycorrhizal fungi, using a light microscope. Root tissue was fixed in glutaraldehyde and osmium for TEM using a previously published protocol (Scott and Larson 1984), to describe and compare cellular morphology of roots from healthy and declining trees.

Results and Discussion

Preliminary results clearly demonstrate a relationship between the degree of sugar maple crown decline and the amount of VAM infection in the trees' roots. Scatter plots of root mycorrhizal infection as a function of tree health reveal similarly shaped third order polynomial regressions for all 3 declining bushes (Fig. 1a-c). These show that for trees of at least moderate health there is an inverse relationship between tree health and VAM colonization. Declining trees, however, show increased mycorrhizal infection, while infection levels of severely declining trees are very low. These trends are more evident in the Ungard and Miller sites which were in a much more critical state of decline than the Alf site at the time of sampling. The combined data from all 3 declining sites were used for the scatter plot in Fig. 2, which shows a second order correlation between the

FIG. 1. Relation between mycorrhizal infection and tree health. (a=Ungard, b=Miller, c=Alf)

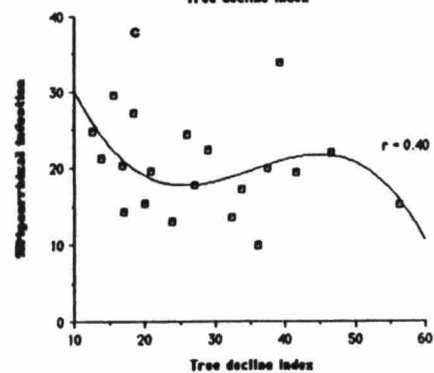
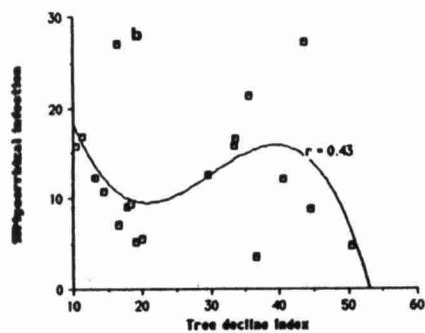
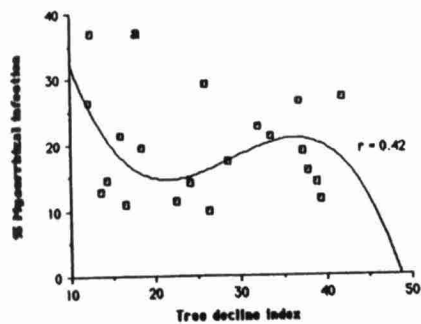
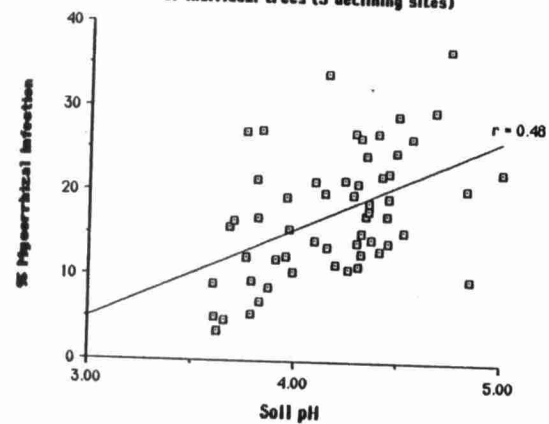


Fig. 2.

Relation between soil pH (A horizon) and mycorrhizal infection of individual trees (3 declining sites)



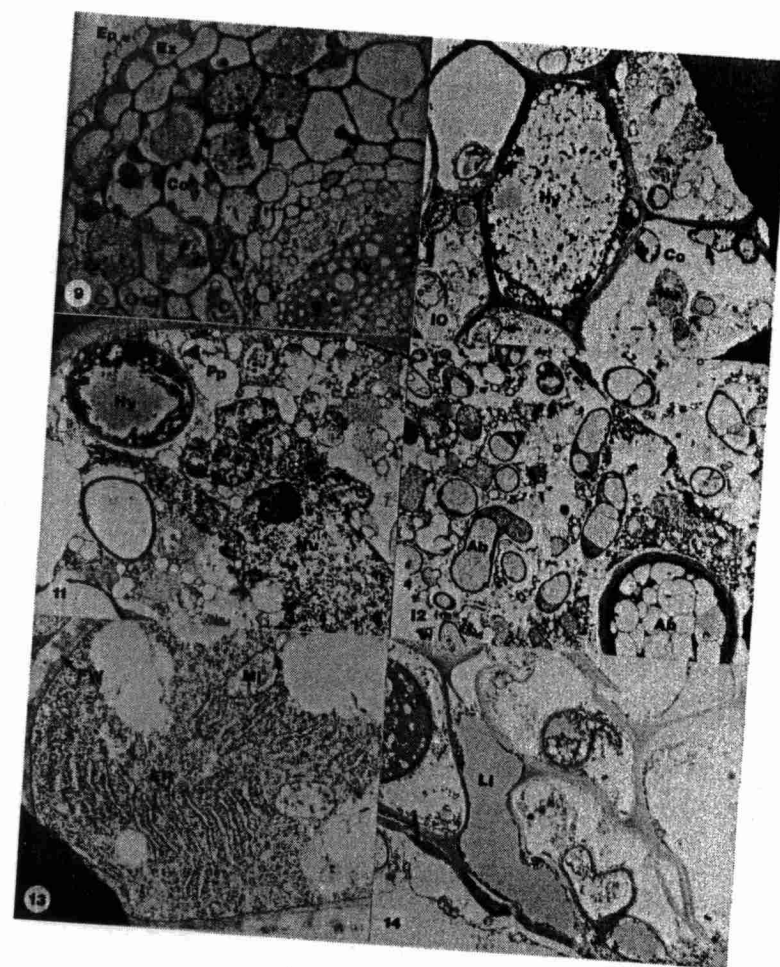
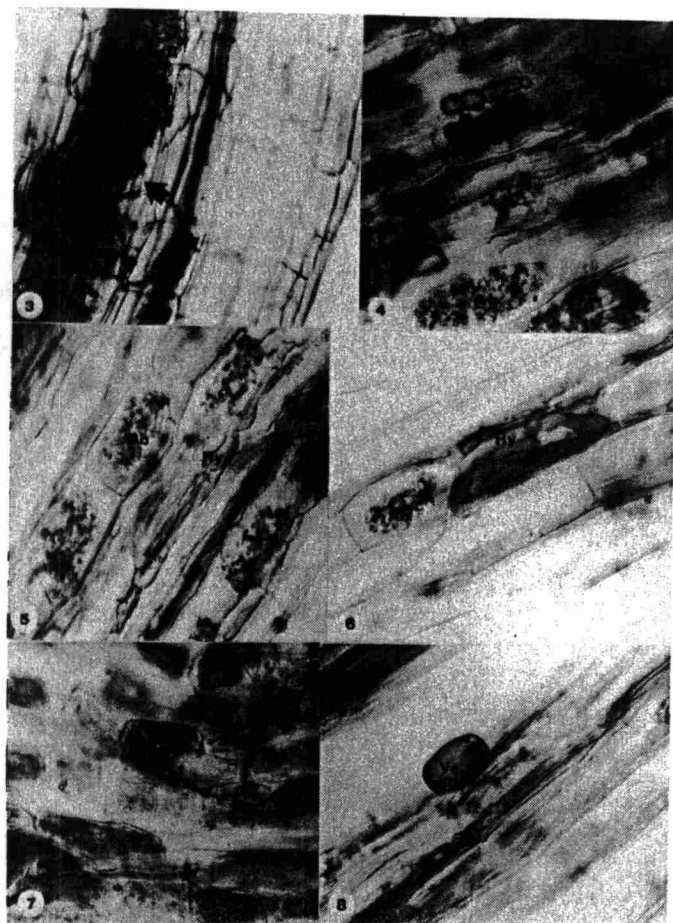
percent of root mycorrhizal infection and soil pH of the A₀ horizon for pH's between 3.00 and 5.00. This may indicate a detrimental effect on the fungal symbiont by soil acidification, either directly or indirectly via a change in the soil microflora resulting in reduced competitive effectiveness of VAM, or via a decreased ability of the trees to support the fungus with assimilates. Mycorrhizal fungal species have been shown to be negatively affected by low pH (Graw 1979; Metzler and Oberwinkler 1987), and field studies have revealed reductions in mycorrhizal communities as a result of acidification (Kumpfer and Heyser 1987; Jansen and van Dobben 1987; Termorshuizen and Schaffers 1987).

Light micrographs of cleared, squashed roots of sugar maple are presented in Plate 1, and show VAM structures similar to those described by Kessler (1966). The darkly stained cells containing VAM structures, as well as clear, uninfected cells are shown in Fig. 3. Figures 4-8 show higher magnifications of VAM structures inside maple roots, including mycorrhizal fungus hyphae, arbuscules and vesicles. Hyphae and arbuscules could usually be observed, while vesicles were abundant in some rootlets and rare in others. Hyphae were frequently seen as coils surrounding cortical cell nuclei (Fig.6).

At the cellular level (Plate 2), Fig. 9 shows bright field microscopy of a cross-section of a typical sugar maple root. The cortical region is heavily infected with VAM and contains abundant tannins. The fine structure of mycorrhizal roots is shown in the TEM micrographs in Figures 10-14. Infected cortical cells contain a highly lobed nucleus (Fig. 11). This altered morphology is thought to be induced by the VAM. A polyphosphate-like substance is seen in some vacuoles in Fig. 11. Hyphae and arbuscules of varying ages and stages of development were observed. In older stages of

Figs.1-6. Light micrographs of cleared, squashed roots of sugar maple (*Acer saccharum*) stained with trypan blue. Roots are, at most, 8 weeks old. Fig.1: A low magnification view showing darkly stained cells containing VAM (arrow), as well as clear, uninfected cells. Figs.2-6: Higher magnifications of VAM, including fungal hyphae (Hy), arbuscules (Ab) and vesicles (Ve).

Figs.7-12. Light and transmission electron micrographs of cross sections of roots of sugar maple. Fig.7: Bright field microscopy of a root cross section stained with TBO, showing a cortical region heavily infected with VAM. Epidermis (Ep); exodermis (Ex); cortex (Co); xylem (Xy). Fig.8: Cortical cells contain hyphae (Hy, black arrows) of varying diameters and age. Older hyphae are filled with lipid. Nuclei (Nu) can be seen in several of the cortical cells. Fig.9. An infected cortical cell containing a highly lobed nucleus (Nu). This altered morphology is thought to be induced by the VAM. Small vacuoles contain a polyphosphate-like substance (Pp). Fig.10. A cross section through a branched arbuscule (Ab). Fine branches are vacuolated and contain a granular electron-dense deposit. Fig.11. High magnification TEM of the fungal cytoplasm showing numerous profiles of endoplasmic reticulum (ER) and mitochondria (Mi). The fungal wall (FW) is degraded in appearance. Fig.12. Cortical cells may contain aging hyphae with large lipid deposits (Li).



arbuscule formation the numbers of fine branch hyphae increase until much of the cortical cell is filled. Fine branches are vacuolated and contain a granular electron-dense deposit (Fig. 12). Older hyphae are filled with lipid (Fig. 14). Several points of penetration of external hyphae were common along a short length (1 cm) of root and caused overlapping of developmental stages of the fungus. Morphological features of the fungus cytoplasm such as the endoplasmic reticulum and mitochondria seen at the highest magnification in Fig. 13, imply metabolically active fungal tissue.

An important aspect of the TEM study in addition to describing sugar maple roots at the TEM level, which has never been reported, is to compare the fine structure of roots of declining and healthy trees. Early indications show that the root tissue of healthy trees did not preserve as well as root tissues of declining trees (i.e. the fixative penetrated better into declining roots), which may in itself be an indication of breakdown or changes in the cell walls or membranes in declining roots. More root tissue needs to be sectioned and examined to see if this is the case.

In the root ingrowth study we found mycorrhizal infection to be increased in slight to moderately declining sugar maple trees compared with healthy trees, and significantly decreased in the trees with severely declining crowns (Table 1). These results quite closely support the findings for the mycorrhizal infection of roots sampled in the first study; thus, different trees, different ages of roots, different sampling techniques and different years of sampling gave us the same pattern of significantly increased mycorrhizal infection in declining trees, but very low levels of infection in severely declining trees.

In the ingrowth core study preliminary results in Table 1 do not show a relationship between the type of soil (either healthy or declining) in the

Table 1. Preliminary data on mycorrhizal infection of sugar fine roots in ingrowth cores containing soils from beneath trees in three categories of decline severity.

Decline index class*	Number of trees	Soil in root bag	Percent mycorrhizal infection ($\bar{x} \pm SD$) [†]
DI < 40	9	healthy soil declining soil	19 $\pm$ 22 17 $\pm$ 14
DI 40 - 60	4	healthy soil declining soil	53 $\pm$ 21 45 $\pm$ 16
DI > 60	2	healthy soil declining soil	12 15

* DI < 40 - healthy tree DI 40-60 - declining tree
DI > 60 - severely declining

Decline indices incorporate loss of crown cover.

[†] Scoring based on number of VAM infected mm of cleared root tissue of the total mm examined for 6 roots/soil treatment per tree. Data are for the Miller site, and the fertilized and steam-sterilized treatments of declining and healthy soil have not as yet been scored.

mesh bags and the degree of mycorrhizal infection. However, the 8 week period in which the roots grew in the different soils may not be long enough to see an effect of soil chemistry on the developing mycorrhizal infection. Furthermore, the fungal inoculum may come primarily from the tree roots as they develop into the bags rather than from the soil itself, particularly since the soils with which the cores were filled were air-dried and sieved in the laboratory to remove any roots.

Strong differences occurred in the concentrations of elements in soils taken under either healthy or declining sugar maple trees (Table 2). The soil from declining trees had significantly lower levels of Ca, Mg and Mn for the Miller site, while for the Ungard site these same three nutrients, as well as P were significantly reduced, and Al was slightly higher in the declining soil. Surprisingly, for the Miller site the declining soil contained significantly higher P than the healthy soil; this finding is in contrast to previous analyses by Kinch and Hutchinson (unpub.) showing much lower P levels in the declining Miller tree soil compared to the healthy tree soil. A possible explanation is that the soil was collected in early May in the current study for the root bags, whereas in the work by Kinch and Hutchinson soil was collected in the summer and in the fall. Soil from the declining trees may release nutrients from the litter from the previous fall at a slower rate, combined with a greater uptake of P by healthy trees in the healthy area of this site when the roots begin to grow actively in April and May. The Ungard site was in a less critical state of decline than the Miller site at the time of this study and these seasonal shifts in P, from being higher in declining soils in early spring to lower in declining soils in the summer and fall were not seen.

The declining soils from both sites caused a dramatic reduction in root

Table II. Differences in the chemical characteristics of surface soils below either healthy or declining sugar maple trees at two Ontario sites. (Concentrations (mg/l) of elements in a 1:10 soil:water extract)

Soil health	pH	P	Ca	Mg	Al	Mn	S
Ungard							
Healthy	4.5	80±2	443±190	62±22	15±1	76±35	78±1
Declining	4.2	46±6	55±4	9±1	23±4	9±1	68±3
Miller							
Healthy	4.0	48±3	229±22	46±4	22±1	115±9	97±6
Declining	4.0	118±9	97±9	26±3	23±2	15±2	104±8

Values are the mean ± 1 standard deviation, n=3.

Table III. Calcium concentration (mg/l) of roots of healthy and declining trees from Miller growing into ingrowth cores containing different soils.

Tree health*	Soil health and treatment			
	Healthy	Declining	Healthy fertilized	Declining fertilized
Healthy (DI-10-40)	4972	4019	5793	5105
Declining (DI-50-70)	3752	3385	4634	4602

* DI - decline index

Decline indices incorporate loss of crown cover.

Values are the mean of roots from 5 trees. For each tree, roots from 3 replicate ingrowth cores were homogenized and pooled.

growth into the mesh bags compared with bags containing the healthy soils (data not shown). These data show that the actual chemical state of the soil, rather than a reduced assimilate supply from stressed trees, is detrimental to sugar maple root growth. The reduction in levels of important soil nutrients in declining soils, combined in some instances with low pH and elevated Al, could account for the present decline in sugar maple.

Although we cannot entirely eliminate the possibility that a root pathogen, present in the declining soil and not in the healthy soil, is involved in the observed root inhibition two lines of evidence suggest this is not the case: (1) steam-sterilization of declining soil gave only a small (non-significant) increase in root biomass in the ingrowth core study (data not shown) and (2) preliminary microscopic examination has shown a number of non-mycorrhizal fungal species, possibly pathogenic, attached to roots, but these are seldom in abundance on the roots and as well they are observed on both healthy and declining tree roots.

Data for the chemistry of roots from Miller showed that Ca is significantly lower in roots of declining trees than healthy trees (Table 3). Furthermore, Ca concentrations were increased when roots grew into healthy tree soil, compared to the declining tree soil. The fertilizer treatment of superphosphate (P_2O_5) and gypsum ($CaSO_4$) increased the calcium levels in every case. Although not all of the elemental analyses are complete other important elements in the roots, including P, Mg and K, showed no response to the different soils. These results clearly show that Ca deficiency is a major factor inhibiting root growth of sugar maples at this site. Other results from various seedling experiments in our laboratory (Hutchinson and Adams unpub.; Kinch and Hutchinson unpub.) have shown that seedlings grown on declining tree soils for various Ontario and Quebec sites have deficiencies

of Ca, Mg, Mn or P or any combination of these four. Aluminum was significantly higher in seedlings grown on the declining tree soil for some of the sites we examined.

Calcium plays an important role in cell wall structure and wall integrity in plants. It is interesting to speculate that the very low calcium levels associated with roots of declining trees may account for the significant increase in mycorrhizal infection levels in moderately declining trees, via either easier hyphal penetration or increased leakiness of the membranes to the carbohydrates and sugars the fungus needs to thrive. Rather than the normal symbiotic relationship, the mycorrhizal fungus may actually become parasitic on roots of the declining trees. The severe drop in infection in trees showing advanced stages of decline may show that trees in poor condition can no longer support mycorrhizae, leading to the further demise of the tree.

In conclusion, the findings from this work to date show that an alteration in the mycorrhizal infection of declining sugar maple trees, as well lower levels of calcium in declining tree roots could account for their present decline. Soils collected under declining trees were lower in Ca, P, Mg and Mn, and elevated in Al, compared with soils beneath healthy trees, and substantially reduced maple root growth.

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